HIGH-ELEVATION SPECIES CLUSTERS IN THE ENCHANTMENT LAKES BASIN, WASHINGTON

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ABSTRACT

Subalpine and alpine vegetation from the Enchantment Lakes Basin was analyzed by species classification methods (Q-mode or inverse analysis) to determine groups of species that cooccur. It was possible to make environmental interpretations of these groups consistent with the known habitat preferences of each species within the group. Eleven groups were identified in the subalpine. Three indicate different forest conditions; two indicate wet, open forests; three suggest different rocky, open, low-elevation habitats; and three indicate krummholz habitats. In the alpine 14 groups fall into five categories: one indicates acid soils; three indicate wet to mesic meadows; four indicate seasonally dry meadows at various elevations; three indicate mesic to dry fell-fields; and three indicate xeric fell-fields and talus. Species composition of each group is given. It is concluded that species classification is a useful tool even when not combined with stand classification (R-mode or normal analysis). It enhances the investigator's ability to detect species valuable as indicators and is useful in experimental design.

The high elevations of the east-central Cascades are receiving increasing recreational stress. The creation of the Alpine Lakes Wilderness Area will intensify impact in fragile high-elevation ecosystems by making the region and its qualities better known to hikers, yet the vegetation of the alpine portions of this region remains little known. Douglas (1972) studied subalpine vegetation of the mesic North Cascades, while Douglas and Bliss (1977) studied high-elevation meadow vegetation across the North Cascades. They described a number of communities similar to those in the Enchantment Lakes Basin. Data from their Table 2 (Douglas and Bliss, 1977, p. 120–123) provide a partial basis for assessment of some of my results.

The present objectives are to identify natural groups of species, to relate the species to habitats, and to suggest the basis for ecological group affinities. This analysis facilitates ecological interpretations of plant communities, identifies indicator species, is useful for subsequent research design, and provides information for management.

Inverse analysis has been used in many studies since its introduction by Williams and Lambert (1961). Typically it is used in conjunction with site classification (normal analysis) and when the two are combined, the approach is analogous to the differential tables produced by the Zurich-Montpellier methods (Westhof and van der Maarel, 1978; Holzner et al., 1978). The use of inverse analysis alone, henceforth termed "species classification", has not been widely reported, yet it offers an efficient tool to develop species groups with predictive value.

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METHODS

Field studies. The study area is located in the Wenatchee Mountains, a southeast-trending spur of the Cascade Range dominated by Mt. Stuart, a granodiorite batholith reaching 2889 m. The vegetation of portions of montane and subalpine slopes in this region has been described by del Moral (1974, 1975; del Moral et al., 1976; and del Moral and Watson, 1978). The Enchantment Lakes Basin is on the southeastern shoulder and contains eight large lakes and many ponds. Elevations range from 2060 m in the lower basin to over 2600 m on the peaks surrounding the upper basin. Forest and meadow vegetation interdigitate in response to physiographic factors. The vegetation is described elsewhere (del Moral, 1979).

The growing season becomes progressively shorter with increasing elevation, but is controlled locally by snow accumulation, melt patterns, exposure, wind, and frost. No climatic records exist for this basin; year-to-year fluctuations are large and are affected by the amount of winter snow and the frequency and amount of summer rain. The vegetation was in excellent condition and nearly all species were reproductive at the time of this survey. The Mt. Stuart granodiorite is the parent material of all soils in this basin. Soils differ in maturity and organic matter in response to drainage and erosion patterns.

The vegetation was sampled for species presence in 199 plots. Approximate plot locations were determined from topographic maps and aerial photographs, but the exact location was determined subjectively in the field to maximize within-plot homogeneity. The plots were distributed on the landscape so as to encompass the full range of accessible habitat variability. Forest plots were 10 × 20 m and meadow plots were 10 × 10 m. All vascular plant species within the plots were recorded (nomenclature follows Hitchcock and Cronquist, 1973). Plot location, elevation, slope, aspect, and soil characteristics were recorded. Moisture status of each site was estimated on a five-point scale from topographic, edaphic, and location factors. Exposure to wind and proximity to persistent snow banks were factors of major importance.

Analytical methods. Species classification reveals groups of species with similar local distributions that may reflect similar ecological or physiological properties. It is a procedure reciprocal to vegetation classification. Species classification has been termed inverse analysis (Williams and Lambert, 1961) and Q-mode analysis (cf. Mueller-Dombois and Ellenberg, 1974). The R-Q notation is fraught with interpretational difficulties and is best avoided.

Species classification can be affected by measures of abundance or dominance. Therefore, I used only presence-absence data in this study.

The 199 plots were divided into 113 with tree species (subalpine) and 86 lacking trees (alpine) and were analyzed separately.

Species were classified into groups with similar distribution patterns using two cluster methods. DIVINF divides species into groups based on their mutual occurrences in key plots (Williams, 1976) and therefore may mis-associate a species characteristic of one habitat that fortuitously occurs in a plot diagnostic of another habitat type. MULTBET merges a pair (or group) of species with the most similar distributional pattern in a series of agglomerative steps (Lance and Williams, 1967). Species with only one occurrence were eliminated. Because the results of the two algorithms were similar, I report a synthesis of the two, drawing upon the works cited below to resolve ambiguities. Of species classified by both methods, 73 percent of the subalpine and 74 percent of the alpine species are in identical groups, while only 5.5 percent and 4.5 percent, respectively, indicate different habitats. These seven discrepancies involve rare species. The remaining cases indicate similar habitat conditions.

Ecological interpretations of the species groups are inferred from Hitchcock and Cronquist (1973), Franklin and Dyrness (1973), del Moral (1974, 1975, 1979), del Moral et al. (1976), Douglas and Bliss (1977), del Moral and Watson (1978), and from the habitat characteristics of plots in which the species cooccur, especially diagnostic plots identified by DIVINF.

Results

A total of 101 species could be grouped by the analytical procedures. The more useful species groups are those that consist of species with moderately wide distributions. These groups indicate fairly precise habitat conditions yet are sufficiently widespread to have meaning beyond the narrow confines of the study area. Groups consisting of very widely distributed community dominants are less informative.

Subalpine

Eighty-one of 102 species in the subalpine were classified into 11 groups. Those not classified are rare and have little indicator value. Parenthetical numbers after each species are the number of occurrences. An asterisk indicates a species whose habitat characterization agrees with that of Douglas and Bliss (1977) and a plus indicates a disagreement with those authors.

Group A. *Picea engelmannii* (25), *Ledum glandulosum* (22), *Saxifraga ferruginea* (22), and *Pedicularis ornithorhyncha* (8): cold wet forests around 2300 m in which standing or running water can be found.

Group B. *Pinus albicaulis* (104), *Larix lyallii* (90), *Abies lasiocarpa* (86), **Vaccinium myrtillus* (70), *Luzula hitchcockii* (66), **Cassiope* *mertensiana* (61), **Phyllodoce empetriformis* (58), **Luetkea pectinata* (43), **Vaccinium deliciosum* (13): and *Kalmia microphylla* (4): cool, mesic forest conditions on acid soils. These conditions are widely encountered in the closed forests of the lower basin below 2300 m.

Group C. **Phlox diffusa* (45), **Carex spectabilis* (43), **Veronica cusickii* (36), **Erigeron peregrinus* (33), *Lupinus polyphyllus* var. *burkeii* (33), and **Hieracium gracile* (31): poorly defined, but appears to be unified by species found on warm, moist, low-elevation forest margins in deep soils, often near low-elevation lakes.

Group D. **Carex nigricans* (12) and *Lewisia triphylla* (6): near lakes in wet meadows with scattered conifers.

Group E. *Arnica latifolia* var. *gracilis* (26), *Ligusticum grayii* (9), *Gentiana calycosa* (5), *Cassiope tetragona* (2), and **Valeriana sitchensis* (2): lush subalpine meadows in forest openings below 2200 m; completely lacking in dry meadows.

Group F. **Lupinus lepidus* var. *lobbii* (38), **Phyllodoce glanduliflora* (34), *Poa gracillima* (26), **Arenaria obtusiloba* (22), *Juniperus communis* var. *montanum* (21), *Saxifraga bronchialis* (20), *Carex rossii* (16), *Luzula campestris* var. *multiflora* (8), *Senecio canus* (6), *Festuca ovina* var. *brevifolia* (3), and **Trisetum spicatum* (3): open, dry, rocky sites, often at the margins of sites occupied by Group A.

Group G. **Juncus parryi* (72), **Antennaria alpina* (62), *Poa cusickii* (56), *Penstemon davidsonii* var. *menziesii* (55), *Sedum divergens* (51), and *Lewisia columbiana* (30): rock crevices and on the edges of dry forests; both *Sedum* and *Lewisia* often extend onto dry, sandy soils.

Group H. *Senecio cymbalarioides* (9), *Saxifraga integrifolia* var. *apetala* (3), *Cystopteris fragilis* (2), and *Epilobium latifolium* (2): infrequent, occurring in well-drained soils or rock crevices that remain wet for much of the growing season due to melting snows.

Group I. *Carex proposita* (47), **Penstemon procerus* var. *tolmiei* (35), **Erigeron aureus* (34), *Arabis lyallii* (29), *Artemisia trifurcata* (27), **Arenaria capillaris* var. *americana* (25), *Aster alpigenus* (22), *Spraguea umbellata* var. *caudicifera* (20), and **Eriogonum pyrolaefolium* var. *coryphaeum* (17): exposed, open forests above 2300 m. Most are prostrate, glaucous, or hirsute and have xeromorphic leaves.

Group J. **Carex nardina* (11), *Castilleja elmeri* (10), *Polemonium pulcherrimum* var. *calycinum* (10), *Phlox pulvinata* (9) **Agoseris glauca* var. *dasycephala* (6), **Silene acaulis* var. *exscapa* (6), *Draba paysonii* var. *treleasii* (5), *Campanula scabrella* (4), **Erigeron compositus* var. *discoideus* (4), **Smelowskia calycina* (4), *Eriogonum umbellatum* var. *hausknechtii* (3), *Polemonium elegans* (3), *Potentilla gracilis* var. *glabrata* (3), *Senecio pauperculus* (3), and *Eriogonum ovalifolium* var. *nivale* (2): primarily alpine species confined to krummholz and granite outcrops generally above 2300 m. Sites are characterized by early snow melt, extreme temperatures, and high wind.

Group K. *Polygonum minimum* (10), **Sibbaldia procumbens,* (7), *Hieracium albertinum* (6), *Castilleja miniata* (5), and **Arctostaphylos nevadensis* (3): dry, open, rocky sites that fail to receive significant snow melt.

Alpine

Analysis of the alpine vegetation grouped 84 species into 14 groups. Eighteen species were not classified. Drought and snow-melt patterns help govern the species patterns in these meadows and fell-fields.

Group L. **Phyllodoce empetriformis* (35) and **Cassiope mertensiana* (30): low-elevation, dry forest margins and progressively wetter sites at higher elevations.

Group M. *Kalmia microphylla* (11), *Saxifraga ferruginea* (10), *Pedicularis groenlandica* (8), *Ledum glandulosum* (7), **Sedum roseum* (7), *Castilleja miniata* (4), *Dodecatheon jeffreyi* (4), and *Ligusticum grayii* (3): very wet to boggy or muddy meadows; *Kalmia, Dodecatheon, Ledum,* and *Pedicularis* require moist soil throughout the growing season.

Group N. **Lupinus lepidus* var. *lobbii* (68), **Erigeron aureus* (49), *Sedum divergens* (41), *Artemisia trifurcata* (40), *Phyllodoce glanduliflora* (39), *Carex proposita* (32), *Luzula campestris* var. *multiflora* (32), and +*Vaccinium caespitosum* (8): generally widespread, occurring in relatively dry subalpine to alpine, deep-soiled meadows.

Group O. **Erigeron peregrinus* (41), **Veronica cusickii* (31), **Salix cascadensis* (27), and *Pedicularis ornithorhyncha* (18): lush meadows above 2300 m.

Group P. *Penstemon davidsonii* var. *menziesii* (24), *Oxyria digyna* (20), **Trisetum spicatum* (16), *Poa gracillima* (15), **Festuca ovina* var. *brevifolia* (14), *Phacelia sericea* (14), **Achillea millefolium* var. *alpicola* (13), *Senecio pauperculus* (13), *Epilobium alpinum* (10), **Saxifraga tolmiei* (9), *Cryptogramma crispa* (3): rock outcrops or gravelly soils that receive snow melt. *Cryptogramma* and *Oxyria* are confined to crevices.

Group Q. **Hieracium gracile* (22), **Luetkea pectinata* (22), *Aster alpigenus* (12), *Lomatium brandegei* (7), *Arnica latifolia* (6), *Lewisia columbiana* (5), and *Polemonium pulcherrimum* (4): low elevation, mesic meadows and rock margins. Several of these species are aggressive colonizers and indicate moderately disturbed sites.

Group R. **Carex nigricans* (22), *Gentiana calycosa* (17), *Lupinus polyphyllus* var. *burkeii* (14), *Senecio cymbalarioides* (13), *Lewisia pygmaea* (12), *Phleum alpinum* (12), and *Potentilla flabellifolia* (12): seasonally wet meadows, dry hummocks within ever-wet meadows, and along stream margins. The habitat is therefore moist for most of the growing season.

Group S. **Penstemon procerus* var. *tolmiei* (44), **Phlox diffusa* (33), *Arenaria capillaris* var. *americana* (25), **Eriogonum pyrolifolium* var. *coryphaeum* (25), *Castilleja elmeri* (23), *Campanula scabrella* (17), and *Carex scirpoidea* (4): rocky margins of graminoid-dominated, high elevation, mesic meadows. The species are somewhat xeromorphic.

Group T. **Antennaria alpina* (73), **Carex spectabilis* (65), *Poa cusickii* (63), **Juncus parryi* (54), and *Luzula hitchcockii* (44): widespread, but most common in high-elevation, sparsely vegetated meadows where snow often persists until August. However, they will coocur wherever vegetation cover is low.

Group U. **Erigeron compositus* var. *discoideus* (19), *Carex rossii* (10), *Saxifraga caespitosa* (7), and *Juniperus communis* var. *montana* (6): dry, rocky meadows, except that *Saxifraga* is confined to moister microsites in such places.

Group V. *Heuchera cylindrica* var. *alpina* (6), *Erigeron compositus* (undescribed variant) (5), *Epilobium angustifolium* (4), and *Polygonum minimum* (4): relatively rare species, in dry, rocky sites showing evidence of recent disturbance (as from rock fall and avalanches). Probably the best indicators of physical disturbance.

Group W. **Carex nardina* (13), **Smelowskia calycina* (8), and **Dryas octopetala* (4): extreme alpine fell-fields above 2400 m with thin soils and low nutrients levels.

Group X. *Saxifraga bronchialis* (17), *Phlox pulvinata* (16), *Potentilla gracilis* var. *glabrata* (14), **Sibbaldia procumbens* (11), **Silene acaulis* var. *exscapa* (10), *Saxifraga integrifolia* var. *apetala* (9), *Geum rossii* (8), *+Carex breweri* var. *paddoensis* (7), and *Eriogonum umbellatum* var. *hausknechtii* (3): high-elevation fell-fields, particularly in exposed sites. Except for the sedge, they are low rosette or mat-forming species.

Group Y. *Arabis lyallii* (36), *Senecio canus* (23), *Draba paysonii* var. *treleasii* (21), and *Eriogonum ovalifolium* var. *nivale* (14): high, xeric fell-fields; prostrate, rosette-forming species adapted to drought and a short growing season, these species fail to occur in more productive meadows where competition presumably is more severe.

Discussion

Species comparisons. There is good agreement between habitat descriptions in Hitchcock and Cronquist (1973), the interpretations of Douglas and Bliss (1977), and those inferred here from species classification.

There are 66 species assigned to both subalpine and alpine groups Of these, 27 occur in relatively less severe habitats in the alpine than they do in the subalpine (e.g., *Antennaria alpina, Artemisia trifurcata, Carex proposita, Erigeron aureus,* and *Veronica cusickii*). Such a trend is common in ecological studies (Whittaker, 1967; del Moral and Watson, 1978) and it is reassuring that species classification reveals this general trend. Nine species (e.g., *Arenaria obtusiloba, Phlox dif-*

fusa, and *Senecio canus*) occur in drier habitats in the alpine than in the subalpine. Such shifts may reflect ecological compensation, in that relatively drier habitats at high elevation may provide as much effective moisture as wetter habitats in warmer sites. None of these shifts is pronounced. Many species of distinctly wet habitats (e.g., *Ledum glandulosum* and *Pedicularis ornithorhyncha*) and of dry habitats (e.g., *Carex nardina, Draba paysonii* var. *treleasii,* and *Poa cusickii*) do not change their relative positions.

There are 37 species classified in this study for which Douglas and Bliss (1977) record prominence values. There are only two cases in which my interpretations disagree with theirs. *Carex breweri* var. *paddoensis,* which I characterize as a species of dry meadows, is viewed by Douglas and Bliss as a species of concave slopes that become dry only at the end of the growing season. These interpretations may be compatible. *Vaccinium caespitosum* is too rare and variable in my study to give weight to my interpretation. The remaining 35 species are characterized in a way consistent with the results of Douglas and Bliss. Only presence/absence data were required.

Comparisons of the classifications. The smaller number of groups (from a larger number of plots) in the subalpine suggests that trees reduce habitat variability. In the alpine plots, relatively subtle microtopographic features result in significant habitat changes. Alternatively, species may display broader ecological amplitudes in the subalpine than in the alpine.

Species composition of groups changes substantially from subalpine to alpine, but these changes usually do not result in grossly different juxtapositions of species. For example, *Artemisia trifurcata* occurs with eight species in the subalpine and nine in the alpine, only two of which (*Carex proposita* and *Erigeron aureus*) occur in both groups. However, the remaining species indicate generally similar habitat conditions.

The subalpine plots fall into four broad ecological categories: forest sites (groups A, B, C); wet forest openings (groups D, E); rocky, open, low-elevation habitats (groups F, G, H); and rocky, xeric, krummholz habitats (groups I, J, K). The alpine groups fall into five categories: shrub-dominated acid meadows (group L); wet to mesic meadows (groups M, N, O); seasonally dry meadows (groups P, Q, R, S); alpine fell-fields (groups T, U, V); and xeric, alpine fell-fields and crevices (groups W, X, Y).

These results can be extended with caution beyond the study area provided that physiographic and physiognomic conditions remain similar and biogeographic effects do not become important.

Evaluation. The interpretations presented in this paper result from a largely unconscious interplay between the analytical results and the author's experience. Habitat characteristics of many of these species are well known to any field ecologist familiar with the region. However the numerical procedures serve to formalize what is known intuitively, to add species to the list of those formally or informally categorized, and to sharpen distinctions between and indicator value of the species in question.

Species groups are abstract collections of ecologically compatible species. In highly variable topography, it is often not possible to rely on a single species for ecological indications, so that the presence of a collection of species adds weight to the determinations. Species groups can and do show overlapping distributions and members of several groups can occur in a single plot (Williams and Lambert, 1961; Webb et al., 1970; Mueller-Dombois and Ellenberg, 1974). In such cases, the group indicating the most restricted set of conditions will provide the most information.

Species classification can be used for several phytosociological purposes. These include: 1) to determine characteristic plots on which to focus experimental work; 2) to clarify the indicator value of particular species; 3) to suggest indicator value of additional species; 4) to identify species with similar adaptive modes; and 5) to select typical or characteristic species for detailed experimental study.

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